THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 51, No. 15, pp. 483-500 September 27, 1978

Ecology and Exploitation of *Ctenosaura similis*

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ABSTRACT

The giant herbivorous iguanid *Ctenosaura similis,* of southeastern Mexico and Central America, occurs in open woodland or edge habitat in seasonally dry lowlands. Sexual maturity is attained late in the second year, ovulation occurs about mid-February, and laying of the eggs (mean 43.4, 12-88) occurs about 5 weeks later. Hatchlings appear about mid-May and have tripled in length at the end of the first year when they are half-grown in length. Females outnumber males 2 to 1; but males are about 1.25 times female length and 1.8 times female weight. Biomass may be several kg per ha (1.67 per ha on a 10 ha sample area in Belize). Each ctenosaur centers its activity at a lookout and shelter; typical foraging radii are from 18.7 m in first-year young to 43.0 m in adult males. Food consists of many kinds of foliage, flowers and fruits, and some animal matter including small rodents, lizards, eggs, and insects. Exploitation of the ctenosaur is heavy in some parts of its range, including Nicaragua, where the species is a common article of diet for country people and also is sold by the hundreds in city markets. As a result, numbers have decreased drastically. Conservation is needed, especially protection of reproductive females, to assure a sustained yield of the flesh, a valuable natural resource.

INTRODUCTION

Ctenosaura similis, a giant iguanid lizard of southeastern Mexico and Central America, is of extraordinary interest eco-

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logically, being important in some areas as a game animal, as a source of high grade protein food for people and, at times, as a pest. Thus, and because it is an abundant and highly conspicuous member of the Middle American herpetofauna, we independently undertook ecological studies of it in Costa Rica and in Belize, respectively. Subsequently, we combined our efforts in a field study which centered in western Nicaragua and was encouraged and funded by the Banco Central of Managua, Nicaragua.

There, we investigated conservation oriented aspects of the ecology not included in our earlier studies, with attention to exploitation, past and present. Although further field work is desirable, the findings presented here will provide some basis for a general understanding of the ctenosaur's basic ecology, of its actual and potential value as a natural resource and of the measures necessary to preserve thriving populations with a sustained annual yield. We have here combined and integrated diverse data obtained from various localities over a 10-year period, for that purpose.

MATERIALS AND METHODS

In Costa Rica, from October 1967 to August 1971, intermittently, Fitch studied local populations at Quepos and Boca de Barranca, Puntarenas Province, and at Finca Taboga and Playas del Coco, Guanacaste Province, with casual observations elsewhere. The lizards, chiefly first-year young, were individually marked by toe-clipping. Measurements (S-V, tail) were recorded to the nearest millimeter and exact location was noted in each instance. Length was estimated for all those sighted from a car. At Belize City, in 1970-1971, Henderson (1973) also studied ctenosaurs by mark and recapture technique and observed the behavior and movements of recognizable individuals over periods of months. Our joint study in Nicaragua in February, March and April, 1976, involved examining ctenosaurs at city *mercados* (N=827), and purchasing selected individuals (N=114) for examining gonads, and finding and interviewing professional hunters who supplied the city vendors. Those and others who hunted the lizards for home consumption provided information about ctenosaurs' population trends, local habits and the methods of securing them. Also, we collected series (N=160) for dissection and examination of stomach contents and gonads.

ACKNOWLEDGMENTS

We are indebted to Sr. Jaime Villa of Managua, Nicaragua, for advice and material aid of various sorts. Mr. Allen Porter, a U.S. Peace Corps Volunteer, assisted us in the field in nearly all phases of the work and carried on with the project in our absence during late March and April, 1976. We thank the Banco Central of Managua and particularly Dr. Jaime Incer and Sr. Roberto Incer of that institution for funding our field study. The Central Nicaraguan government's Catastro expedited our field work by making available a jeep and driver.

ECOLOGY

Habitat: Over its extensive range, in Mexico east of the Isthmus of Tehauntepec, and Central America, *Ctenosaura similis* occurs in varied climates and plant formations, but it is absent from primary rain forest and from cool climates at high altitudes. One seen as a road kill, in June 1968, at Río Itiquis, Costa Rica Highway No. 1, Alajuela Province, approximately 900 m elevation was probably near the upper edge of the species' occurrence. The species is most prevalent on the relatively arid Pacific versant of Central America, but it intrudes onto the Caribbean versant and even reaches the Caribbean Coast and various small islands of the Continental Shelf in the western Caribbean.

The optimal habitat seems to be arid savanna. In Guanacaste Province, northwestern Costa Rica, and in Chinandega, León and Managua provinces, western Nicaragua, we observed high population densities in the dry season in areas made relatively barren by heavy grazing and/or annual burning of dead vegetation. Broken terrain with scattered, large trees, logs, loose boulders, rock outcrops, gullies with cutbanks, or streams with riparian thickets, provided the required shelter. Lava fields with a sparse vegetation are inhabited.

Ctenosaurs have often been found closely associated with cattle at corrals, salt blocks, and pasture edges. Such barren places provide the lizards with enough food from low weedy vegetation missed by the cattle and from foliage and flowers of trees.

Rock walls provide a superabundance of shelter and may have unusual concentrations of ctenosaurs. Fence posts, especially if large and hollow, are used both for basking and for shelter. Ctenosaurs often live on the margins of cultivated fields feeding on the crops and also on weeds.

The disturbed and seral conditions resulting from human activities often favor survival and increase of the ctenosaur, sometimes found living in close association with people. At the village of Playas del Coco in Guanacaste several were seen in a pig sty where they came to eat garbage. On the northern edge of Belize City and at Boca de Barranca, Puntarenas Province, Costa Rica, colonies of ctenosaurs lived among groups of buildings where vegetation was held in check by artificial trimming and by the trampling of large numbers of people (schoolyard, beach resort). Their burrows were beneath buildings. Many ctenosaurs were observed within the city of Managua, Nicaragua, in small, semi-isolated colonies in yards with trees and on roofs. Walled gardens provided an especially secure habitat. Other ctenosaurs lived in vacant lots with trees and grass, or lived among shacks or adjacent to warehouses or ruins where unused machinery, piled lumber, earthquake debris or trash provided shelter.

In the humid Caribbean lowlands, ctenosaurs are relatively scarce and localized in dry and open situations. On Great Corn Island, Zelaya Province, Caribbean Nicaragua, they were observed in forest and thick plantations, and appeared to be much more arboreal that their mainland counterparts. At Belize City, Neill and Allen (1959) found ctenosaurs in mangrove swamps, and Henderson (1973) found adults in the open areas about buildings, but found juveniles in a swampy and brushy adjacent area, often climbing in the bushes.

Burrows: Ctenosaurs dig effectively with alternate strokes of the powerful, clawed forefeet. Some find shelter above ground, in hollow limbs or fence posts, but most dig burrows where they are protected above by such objects as buildings, boulders, or tree roots. Vertical banks of road cuts or eroded gullies also provide favored sites and burrows often have well defined trails leading to them. The holes are flat bottomed, arched above, and wider than high, with winding and sometimes branched tunnels. Several that we excavated were between 1 and 2 m long. Some burrows have cavernous entrances, enlarged by digging predators or eroded by heavy rains. The tunnels are wide enough to permit the lizard to turn around inside and are horizontal or slope gently downward. Various snakes, lizards, rodents and arthropods use ctenosaur burrows for shelter.

Ctenosaurs do not emerge at night or on rainy days. Even when weather is favorable, the lizard does not emerge until well after sunshine has reached the burrow entrance. At first, only the head protrudes, and by gradual stages over perhaps half an hour, more of the body. Finally the lizard scrambles to a nearby lookout to bask where the surface is already warmed by the sun. Only when the body temperature reaches 36°-37° C, is the animal fully active and ready to forage.

The ctenosaur is most active in the morning, retiring underground to escape the midday heat, and often has been seen in the afternoon lying in burrow entrances or back in the tunnels awaiting more favorable lower temperatures.

Each lizard defends its home burrow against intruders, but may use other outlying burrows occasionally or habitually. An individual often shifts from one home burrow to another, and collectively, the burrows are the communal property of the local population.

Social Behavior: Territoriality in *Ctenosaura similis* involves exclusion of others from home burrows and basking places, and maintenance of spacing. Intrusions may cause conflict, with fighting mainly between similar-sized first-year young. A threatening approach is followed by sparring, lunging, biting, and persistent clinging to any part of the opponent that the lizard can seize, while writhing or rolling in an effort to break the other's grip. No noticeable damage was noted from such encounters.

Doubtless the most severe fighting is between large males, but is infrequent because of their relatively small numbers and wide spacing. Over a period of 11 months, Henderson (1973) observed no overt interactions between several adult males that lived beneath the same building on the outskirts of Belize City. There seemed to be mutual avoidance of confrontations by maintenance of spacing. However, when an outsider was brought in and tethered, he was promptly attacked by a dominant resident. After a series of struggles with intervening pauses for rest, the resident male gradually abandoned his attempts to oust the tethered intruder and the latter, when released, remained in the vicinity, taking possession of the burrow and basking site of the resident whom he had outlasted in the territorial confrontation.

The adult females seen always maintained spacing of at least several meters. As in other iguanids, *Crotaphytus* (Fitch, 1956), *Sceloporus* (Blair, 1960), and *Uta* (Tinkle, 1967), there is probably mutual aversion and hostility among females, but with aggressive behavior relatively weak. No female fighting nor pursuits were observed. Adult males were often seen in "consort pair" associations with females that seemed to be based on mutual attraction, but at any time the polygynous male might wander away from his consort and find another temporary mate. Formation of harems was probably prevented by mutually agonistic responses of females.

Each individual, regardless of sex or size, has a territorial center with one or more burrows or basking sites, but territorial boundaries are not well defined. The ctenosaur may spend much time basking at one or a few spots, and finally may move on to a different location without ever having used most of the apparent territorial area near its burrow and lookout. Often, food in the form of succulent vegetation is so abundant that the lizard does not need to spend much time in active foraging nor to venture far.

Where food is abundant, but choice retreats and basking sites are scarce, territories may be partly superimposed, with the same rocks or burrow used by two or more ctenosaurs at different times. Even in such congestion there is not much actual conflict. A smaller, weaker individual automatically avoids a larger, more powerful neighbor and is generally ignored by him. Evans (1951) described social behavior in a colony of *Ctenosaura pectinata* in central Mexico, living in a rock wall around a bean field. Each adult male controlled a section of the wall and adjacent areas, ordinarily excluding other adult males. However, perhaps as a result of abnormal overcrowding, there was much overlapping of territories, and a hierarchical system was superimposed on that of territoriality. A "despot" Alpha male could violate the territory of any other individual with impunity, although in such transgressions mutual threat displays were exchanged between the intruder and the resident. Likewise, other territorial males encroached on the territories of lower ranking individuals. Many subordinate individuals were unable to maintain territories, and avoided the large dominant males.

The somewhat different social structure in the population that we observed at Belize probably resulted from the different situation, rather than specific differences between *C. pectinata* and *C. similis*. At the Belize City cemetery, the relative uniformity in size and distribution of the gravestones that provided shelter, dispersed the ctenosaurs, but at Evans' study area in Mexico, the lack of shelter, except in crevices in the rock wall, concentrated them, leading to frequent, stressful interactions.

Like most other iguanids (Carpenter, 1965), *Ctenosaura similis* displays by stereotyped, species-specific bobbing movements that substitute for actual fighting in most encounters. Henderson (1973) observed and described the display at Belize City consisting of 10-12 vertical bobs of the head with changing rate and amplitude; first, the head was slowly raised to the maximum possible height and then more rapidly lowered; 2 or 3 lower and faster bobs followed, and finally there were 2 or 3 short, quick, upward jerks. The display was often elicited by the sight of a potential rival, and might be given by females and immatures as well as adult males. Also, displays might be elicited by potential threat, such as the approach of a person. At other times the display was given in the absence of any obvious external stimulus, but seemed to reflect excitement or potential danger. It might be given just before or after a shift to a new location.

Movements: Taylor (1956), describing the habits of the species in Costa Rica, wrote: ". . . they may forage a hundred yards or more in varying directions." However, forays are usually less than 100 yards from the burrow as indicated by the homeward dashes of those disturbed in the open by a pedestrian or vehicle. A male in sexual search, a female in search of a site for egg-laying, or a lizard lured by some preferred food in the season of scarcity may venture farther than usual. More often, the same individual will be seen time after time at approximately the same spot. Henderson (1973), observing a small colony in the vicinity of a school building on the outskirts of Belize City, found that most activity is within 1-5 m of the lizard's burrow, but he noted one adult male 88 m from its burrow and recorded several other movements, up to 25 m. Fitch (1973) individually marked many juveniles, mainly in June and July, and recorded 16 recaptures in new locations after periods of weeks. Four relatively long movements were 131, 55, 49 and 46 m; the remaining 12 averaged 10.4 m (4-16).

From 2-7 March 1976, we made observations at the Belize City cemetery on a colony of 49 ctenosaurs. The cemetery was approximately 610 x 200 m bordered on each side (north and south) by a mangrove swamp, and on its west end tapered almost to a point, with a crossroad, swamp, and dense vegetation truncating the lizards' habitat, while at the east end it was bordered by buildings on the edge of Belize. Thus, the population was effectively isolated. Individual movements were further restricted by a well travelled road that bisected the cemetery lengthwise from east to west, and we saw no ctenosaurs venture onto the road. The lizards of this colony, being free from molestation by humans and conditioned to frequent passers-by, were relatively tame and could be easily approached, sometimes to within 1 m, and they could be individually recognized by a combination of size, sex, and peculiarities of color, pattern, tail regeneration, behavior and location. Each lizard had a favorite spot for basking, usually on a tombstone, and had a retreat, usually within or beneath the stone. Most of the tombstones were concrete slabs approximately 2 x 1 x .5 m and many were old, weathered and broken with holes or cracks providing access to the hollow interiors.

Individual ctenosaurs were recorded from 1 to 19 times, but on nearly half the occasions (N=120) were seen at the same place. Movements of less than 3 m were disregarded, because the combined retreat and basking site often spanned approximately this distance. For each ctenosaur movements were recorded as radii between the home base and outlying points visited. For 121 records average was 24.4 m (adult males, 43.0 m, N=22; adult females, 22.55 m, N=38; first-year young, 18.7 m, N=61). Each adult male usually stayed within 1 or 2 m of an adult female. Any ctenosaur, regardless of size or sex, might shift to a different lookout and usually there was a nearby escape shelter.

Use of a specific area by an individual ctenosaur does not conform well with the concept of a typical home range: "The area over which an individual animal habitually travels while engaged in his usual daily activities" (Dice 1952). The ctenosaur spends most of its time at one place and may not stray far from that center while food and other requirements are readily accessible. Feeding and other activities concentrate in the vicinity of the lookout and shelter; degree of utilization is proportional to distance from that home base. The more remote parts of the area that are within the ctenosaur's foraging radius tend to be little used, but outlying, alternative, secondary lookouts with associated shelters permit more thorough use of the area.

For each of the main groups—adult males, adult females and first-year young—radii tend to form a graduated series from the minimum to the maximum. Relatively short movements were most numerous and longer movements fewer. Several of the movements (4 of 22 for adult males, 3 of 38 for adult females, and 3 of 61 for immatures) were abruptly longer and may represent either exceptionally large home ranges or shifts in range. Excluding these few extra long movements, the maximum radii were 58.0 m for adult males, 38.2 for adult females and 48.2 m for immatures. These radii represent circular areas of 1.051, .457 and .731 hectares, respectively.

Food Habits: Although mainly vegetarian, ctenosaurs are known to have taken some animal food including grasshoppers, frogs, young of their own species, a skink, rodents, young chicks and various small birds, a bat and even human feces (Alvarez del Toro, 1960; Tamsitt and Valdivieso, 1963; Taylor, 1956; Fitch et al., 1971; Henderson, 1973).

In February, March and April 1976, we examined 146 stomachs of ctenosaurs collected in western Nicaragua (Table 1). Green foliage from both herbs and trees comprised most of the diet, being present in 76% of stomachs. Succulent plants were relatively scarce in the dry season, especially in the open and barren roadside situations where many ctenosaurs were found. Coarse, seral weeds were often eaten, as they were the most available source of plant food. Many of the lizards living along the edges of cotton fields ate leaves of cotton plants (*Gossypium*). Leaf buds and newly grown tender leaves of trees also made up much of the foliage eaten. A tree about 10 m high in a roadside strip north of Chinandega had lost its foliage when scorched by a grass fire, and new leaf buds were opening at the time of our field work in March 1976. These new leaves seemed especially attractive to ctenosaurs, as we saw several in the tree and shot two, but on the return trip later the same day we saw four, of different sizes, in the tree.

Nearly all flower material in the 146

TABLE 1

FOOD OF CTENOSAURS; CONTENTS OF 146 STOMACHS FROM WESTERN NICARAGUA
FEBRUARY, MARCH AND APRIL 1976

	LEAVES	FLOWERS	FRUITS	SEEDS	MISC. PLANTS	INVERTEBRATES	VERTEBRATES	FECES
Total samples (146)								
Occurrences	111	86	22	11	7	29	11	1
% sample weight ..	47.1	26.2	9.4	4.0	2.3	3.0	4.1	3.9
Adults (73)								
Occurrences	54	45	9	9	5	8	5	1
% sample weight ..	45.2	23.2	10.5	5.5	3.2	2.1	3.8	6.5
Young (73)								
Occurrences	56	42	13	2	1	21	6	....
% sample weight ..	49.0	31.0	8.0	.1	.5	4.8	5.0	....

stomachs was from trees, of kinds which bloom when they are leafless at the height of the dry season. Most were legumes and were yellow, pink or white in that order of frequency. Trees with either flowers or tender foliage sometimes lured ctenosaurs beyond their usual foraging radii. Miscellaneous plant material in the stomachs included stems, and some material too much digested to be recognized in any of the main categories.

Vertebrate prey included small cricetid rodents, *Oryzomys, Scotinomys* (five stomachs), small lizards probably *Sceloporus* and/or *Cnemidophorus* (in two), a partly digested tail of a small ctenosaur (in one) and 9 small lizard eggs probably of *Sceloporus* or *Cnemidophorus,* or possibly *Ameiva* (in one). One adult ctenosaur had a ctenosaur egg, still undigested and with shell intact in its hind gut and another had eaten three such eggs. The presence of such active prey as mice and lizards, and presence of eggs that would have been deposited in burrows, indicate that some of the prey is obtained by digging.

Cannibalism of sorts is indicated by the eating of ctenosaur eggs and tail. Henderson (1973) noted that habitat separation relieves the young from predation by adults. Newly emerged hatchlings may overlap the adults' habitat more than do the scansorial juveniles a few weeks later. However, the active hatchlings are so swift and shy that most apparently escape predatory adults. Young that are several months old become less scansorial and more like adults in habits. They have doubled or even tripled in length, and are larger than the food objects that adults normally take. First-year young that lived in the areas controlled by dominant males occupied lookouts only a few meters from them, but instantly fled when the adults moved toward them.

Invertebrates found in stomachs included 2 lycosid spiders, beetles, butterflies, moths, wasps, bees, dipteran flies, hemipteran "bug," leafhoppers and a grasshopper. Some of the smaller insects made up insignificant proportions of the stomach contents, and probably were ingested secondarily on flowers or other vegetation that the ctenosaurs were eating. Invertebrates were less prominent in the food of the adults than in that of the first-year (8-10 months old) young, although these young were much like adults in habitat and behavior.

Younger, smaller ctenosaurs are much more insectivorous. Near Pisté, Yucatán,

TABLE 2

REPRODUCTIVE STATES OF ADULT FEMALE *Ctenosaura similis* IN FEBRUARY, MARCH AND APRIL, 1976

	Mean sizes of ovarian follicles in individual females	Percentages of females having: ovarian follicles vs.	oviducal eggs	N	Percentages of females having: oviducal eggs or large follicles vs.	recently laid	N
1-10 Feb.	1.5,4,5,7.5,8,9,10(in 3) 12(in 6),15 17,18	90	10	20	100	0	96
11-20 Feb.	....	....	....	....	....	....	....
21 Feb.-1 Mar.	5,11,14,16,16	27	73	22	100	0	90
2-11 Mar.	15.5	14	86	7	100	0	22
12-21 Mar.	....	....	....		93	7	160
22-31 Mar.	....	....	....		78	22	32
1-10 April	....	....	....		6	94	16
11-20 April	....	....	....		....	100	13
21-30 April	....	....	....		....	100	11

Maslin (1963) found stomachs of several juveniles (55-64 mm) filled with insects including fairly large grasshoppers. Allen Porter collected 16 young that probably averaged about 3.5 weeks old (57-80 mm) near Laguna Asososca, León Province, Nicaragua, 28 July 1976, and 15 of the stomachs had insect remains: 23 beetles (scarabaeid, chrysomelid, elaterid, coccinellid), 6 lepidopteran larvae, 3 leafhoppers, 3 ants, 1 gryllid cricket, 1 butterfly and 1 beetle grub. For 32 of the prey items sufficiently intact to be measured or estimated, average length was approximately 10 mm, and prey weight averaged a little less than .09 g. These juvenile ctenosaurs weighed a little less than 10 g on the average, hence prey weight was most often less than 1 per cent of body weight. Although 60% of the items were beetles, some of the prey was of active, swift-moving kinds. Ten of the 16 stomachs had plant material (foliage in 9, yellow flowers in 1, berries in 1) and 59.0% of the food weight was vegetation vs. 41.0% insect prey.

In gardens and cultivated fields ctenosaurs damage plants by nipping off buds, flowers, fruiting heads and tender leaves. Young bean plants are especially liked. Damage may be substantial, and as a result ctenosaurs are generally considered pests and are killed at every opportunity by agriculturalists. Doubtless at some times and places control measures are justified, but harm done to crops seems fairly trivial, weighed against the benefits accruing from utilization of the ctenosaur for food and sport.

Reproduction: Like most other iguanids, *Ctenosaura similis* is oviparous, laying a single clutch of eggs, annually. Early in the dry season in January and February fat bodies are large and ovarian follicles grow rapidly. Follicles are ovulated when they have attained a diameter of 15-18 mm. Table 2 indicates that in the first 10 days of February, 2 of 20 females examined had already ovulated, and 18 contained enlarging follicles, but in 15 of this group follicles were still not mature. In the last 9 days of February (and 1 March) 16 of 27 females had ovulated, 2 others had mature follicles, and three had follicles that were still short of mature size. The last recorded as still having follicles was examined on 10 March. In the last 10 days of March, 7 females dissected had recently oviposited and 25 still had mature oviducal eggs, but all of the 16 dissected in early April were already spent. These records indicate that in 1976 in western Nicaragua, at least, the peak of ovulation occurred in mid-February, and the peak of ovipositing was in late March. Hence, eggs were retained in the oviducts for approximately 5 weeks. Earliest and latest dates recorded for females with oviducal eggs were 4 February and 2 April, respectively. Individuals vary 3-4 weeks in the timing of their reproduction, but *Ctenosaura similis* has a much more concentrated breeding season than any other Middle American lizard that has been studied.

Number of eggs per clutch, determined from enlarged follicles and from oviducal eggs in unlaid clutches of the females dissected in February and March 1976, averaged 43.4 (12-88, N=69). The maximum of 88 distinguishes *C. similis* as one of the more prolific of all lizards, even more so than viviparous species. The wide range of variation between females in numbers of eggs is especially remarkable, and is strongly correlated with age and size of the individual.

In Table 3, reproductive females are divided into 8 size-classes which are believed to be the most plausible bases for cohorts in successive annual age-classes, taking into account the known growth rates of marked individuals and the fact that each annual cohort in a stable natural population is somewhat less numerous than the next younger group. Within each of the female size-classes in Table 3, the clutch size is much less variable than for the group as a whole, and the mean increases from approximately 22 eggs per clutch in the smallest (two-year-old primiparae) to approximately 70 in the largest adults (8-year olds).

The smallest clutch recorded (12) belonged to the smallest ovigerous female of 191 mm snout-vent (s-v) and the largest clutch (88) belonged to one of the four larger females dissected (338 mm s-v). However, a few females deviated markedly from the average clutch size for their size-group, indicating that factors other than body size may strongly influence the number of eggs.

For 40 females in which weight of unlaid oviducal eggs as well as total weight was recorded, clutch weight averaged 21.65% of the total (15.5-36.9%). For the different size-groups of females, averages approximated that of the entire group, with

TABLE 3

Adult Female Ctenosaurs That Were Measured, Grouped in Size-Classes That Correspond with Possible Age-Classes, Showing Correlation of Clutch Size with Size of Female

Size-Class mm S-V	Number measured	Estimated Age (Years)	Clutch size (means and extremes)
191-250	63	2	21.688 ± 1.164 (12-27 in 16)
251-269	51	3	36.000 ± 1.414 (29-41 in 8)
270-284	46	4	40.900 ± 3.321 (29-63 in 10)
285-299	41	5	42.428 ± 2.852 (29-51 in 7)
300-310	37	6	51.571 ± 2.927 (30-66 in 14)
311-326	25	7	61.833 ± 3.534 (49-74 in 6)
327-340	17	8	69.500 ± 3.359 (59-88 in 8)
341-347	3	9	....

no discernible trend toward greater reproductive effort in larger females. In the ctenosaur, the "reproductive strategy" as defined by Tinkle, Wilbur and Tilley (1970) differs from strategies of most tropical lizards (but resembles that of various Temperate Zone lizards) in delayed maturity and in the production of a single annual clutch. It differs from most other lizards, but resembles some other giant iguanids, teiids, and varanids of tropical mainlands in its extremely large clutch, and in low ratio of egg- and hatchling-size to adult.

Fat deposits in the posterior ends of the abdomens were bright yellow and were especially conspicuous in females that had not yet ovulated. In 15 of these females abdominal fat bodies ranged in weight from 4 to 54 grams (.5 to 6.5 per cent of the total weight), with a tendency for those with smallest follicles to have the largest fat bodies. Evidently the fat bodies provide much of the sustenance that permits rapid enlargement of the follicles as yolk is deposited. In three females with approximately full-sized follicles (16-17 mm in diameter), fat bodies averaged 5 per cent of total weight; in nine females with follicles 12-15 mm in diameter, fat bodies averaged 48 per cent of the follicles' weight; and in two females having follicles 10-11 mm in diameter, the fat bodies averaged 169 per cent of the follicles' weight. In females that had ovulated, fat bodies were much shrunken, and in most instances weighed less than one gram. Figure 1 shows the relative weights of the fat bodies and the ovaries in females with enlarging follicles.

Growth: Typical hatchlings are between 55 and 60 mm snout-vent, but some are slightly larger or smaller. As indicated, individual females vary from three to four weeks in the time of laying, so that the earliest hatchlings are as much as 25% longer than their original length by the time the latest appear. In older young, the size difference increases as some make better growth than others. The largest in each of 18 series of 9 to 51 young (Tables 4 and 5) averaged 138.5% of the lengths of the smallest. In series that average more than a month old, the largest may be 50% or more larger than the smallest.

Early growth is best shown by ten series captured at four localities in northwestern Costa Rica in 1968 and early 1969 (Table 4). There were five successive samplings at Playas del Coco and three at Boca de Barranca. Evidently there was some difference between these localities in hatching time, from the first week of May (Boca de Barranca) to the second week (Playas del Coco) or third week (Finca Taboga, Quepos). Hatchlings were first seen on 1 May at Quepos. A single hatchling was seen on 14 May at Taboga; seemingly hatching was just beginning there. Average length gain s-v is usually approximately 4 mm per week or a little less for the first few weeks, but then slows to somewhat less than 3.5 mm per week.

Six young marked in late May and recaptured after intervals of 31 to 36 days, made an average gain of only 2.1 mm per week, probably due to temporary stunting from the adverse effects of toe-clipping. Two other young were recaptured after longer intervals, when they had fully recovered from the adverse effects of marking. From 1 July 1968 to 12 February 1969 one grew from 86 to 143 mm and from 26 August 1968 to 4 February 1969 the other grew from 95 to 170 mm. These gains indicate average growth rates of 1.76 and 3.39 mm per week, respectively, over periods of 32 weeks and 23 weeks.

The lizards of the four Costa Rican localities listed in Table 4 range from 9°25′ to 10°35′ North Latitude and have breeding schedules several weeks advanced over those occurring in more northern parts of

TABLE 4

SIZES OF JUVENILE CTENOSAURS ON VARIOUS DATES AT COSTA RICAN LOCALITIES, SHOWING EARLY GROWTH

DATE	LOCALITY	MEAN LENGTH S-V (MM.)	N	ESTIMATED AGE (WEEKS)	ESTIMATED AVERAGE GAIN (MM.) PER WEEK SINCE HATCHING
20-23 May	Playas del Coco	59.1 (56-63)	24	1	4
27-30 May	Boca de Barranca	70.9 (57-82)	51	3.5	4.2
20 June, 1-3 July	Quepos	76.1 (60-90)	19	5	3.4
29-30 June	Boca de Barranca	83.9 (63-109)	30	8	3.8
7 July	Finca Taboga	87.2 (73-107)	19	7	4.5
9-10 July	Playas del Coco	78.1 (63-97)	21	7	3.3
14-17 Aug.	Playas del Coco	95.5 (78-107)	9	12	3.3
20-30 Aug.	Boca de Barranca	103.9 (80-114)	19	14	3.3
23-26 Aug.	Playas del Coco	104.1 (84-127)	15	13	3.3
4-7 Feb.	Playas del Coco	147.5 (120-165)	12	35	2.6

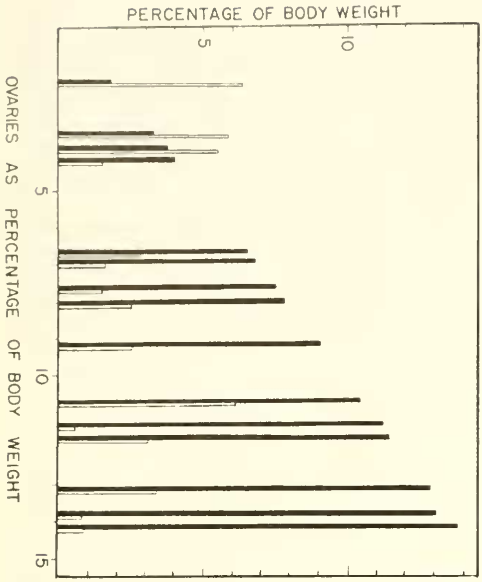
the range. Henderson (1973) found that the young first appear in mid-June in Belize. Table 5 shows average sizes of series of young collected in various parts of the range, with series arranged in order from latest to earliest calculated hatching dates. The data indicate that in some areas hatching may be delayed as much as two months beyond that characteristic of northwestern Costa Rica in lowland areas. The

TABLE 5

SIZES OF FIRST-YEAR *Ctenosaura similis* AT VARIOUS LOCALITIES AND DATES, SHOWING RETARDATION OF SCHEDULES NORTHWARD AND AT HIGHER ELEVATIONS.

LOCALITY	LATITUDE & ALTITUDE*	MEAN LENGTH S-V	RANGE	N	DATE OF COLLECTION	ESTIMATED AVERAGE HATCHING DATE
Tenorio, Guanacaste, Costa Rica	10°37′(650m)	77.25	(72-87)	4	8-23-52	18 July
Tilarán, Guanacaste, Costa Rica	10°28′(562m)	81.0	....	1	8-15-54	11 July
Pisté, Yucatán, Mex.	20°44′	63.0	(53-71)	22	7-20&21-62	7 July
Isla de Ometepe, Lago de Nic.	11°32′	77.7	(65-92)	18	7-30-8- 1-	3 July
Lago Asososca, León, Nic.	11°26′	70.4	(57-80)	16	7-28-76	3 July
Isla de Maiz, Nic.	12°07′	57.5	(60-75)	11	6-29&30-64	19 June
14 km E Rivas, Rivas Nic.	11°26′	80.6	(88-75)	11	7-20-64	9 June
Managua, Nic.	12°08′	66.8	(60-80)	9	6-20&21-56	3 June
Managua, Nic.	12°08′	54.2	(49-59)	9	6-3&4-56	1 June
S. Antonio, Chinandega, Nic.	12°32′	73.7	(63-94)	23	7-5 to 11-64	1 June

* Near sea level, except where otherwise indicated.



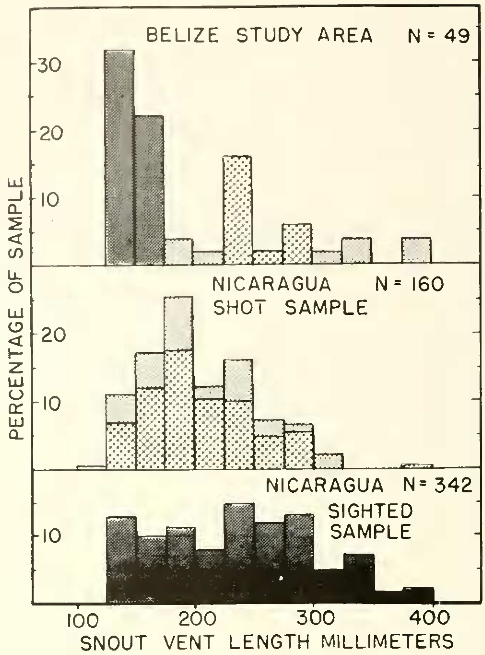


FIG. 1. Relative weights of fat bodies (open columns) and complements of ovarian follicles (solid columns) in 15 female ctenosaurs having their follicles in different stages of growth.

FIG. 2. Size-classes in three population samples of *Ctenosaura similis;* stippled columns represent males, cross-hatched columns represent females and shaded columns represent individuals of undetermined sex.

later dates were for Tenorio and Tilarán, Costa Rica, near the localities of Table 4 but in the relatively cool climates of montane areas. The next were those from Yucatán 1070 km north of the Costa Rican localities. Isla de Ometepe in Lago de Nicaragua and Isla de Maiz in the Caribbean, having relatively cool climates moderated by surrounding water, are also late. Hatching at various localities in western Nicaragua (Rivas, Isla de Ometepe, Managua, Lago de Asososca, San Antonio) is 2 to 6 weeks delayed beyond the time of hatching in the Guanacaste lowlands.

Although the annual schedule of reproduction and growth differs by only a few weeks in different parts of the range, the differences may be critical. The species thrives best in the relatively hot and seasonally dry climates of western Nicaragua and northwestern Costa Rica. In regions with more precipitation, less insolation, and lower air temperature, there is a cumulative retardation; eggs mature later, laying is delayed, incubation requires more time, and the young make less rapid and consistent growth.

Of 16 presumed second-year females, 204-250 mm s-v, collected in western Nicaragua from 6 February to 22 March 1976, 13 were reproductive, having enlarged follicles (4 females), oviducal eggs (7 females), or corpora lutea and enlarged oviducts indicative of recent egg-laying (2 females). The remaining 3, having lengths of 220, 215 and 209 mm s-v, had minute ova and small oviducts. Thus, 18.7% of females in the two-year old size-class were non-reproductive. In other parts of the range where climate is less favorable, postponement of sexual maturity until the third year may be the mode, with consequent major loss of reproductive potential.

In western Nicaragua, 6 February to 5

April 1976, first-year young of 170-189 mm length (females) and 190-197 mm (males) were more numerous than larger or smaller young and probably were modal for their age-group of about 8-10 months. Average growth rates (s-v) from the time of hatching are calculated at about 3.1 mm per week for females and about 3.5 mm for males. However, some young, presumably of approximately the same age, were still as small as 127 mm (female) and 135 mm (male), indicating a wide range among individuals. First-year and second-year young apparently overlap in size mainly in the range 190-200 mm for females and 235-250 mm for males. If 200 mm is considered the upper limit for first-year females (in our sample of 160), 53 fall in this age-class, with a mean length of 171 mm. For males, a criterion of maturity that may separate second-year adolescents from first-year young is length of spines of the dorsal crest. These spines are long and prominent in adult males, but low and flattened in females and juveniles. Individual males of 238, 241 and 248 mm and all that were smaller had short spines (2.5 mm or less), whereas individuals of 239, 240 and 247 mm, and all but one that were larger, had relatively long spines (5 mm or more). If males up to, but not including, 240 mm are considered first-year young, the sample includes 39 of them which average 188 mm.

At the end of the first year, males average aproximately 10 per cent larger than females, and as adolescents and adults they grow about twice as fast as females, judging from maximum lengths s-v of 489 (male) and 347 (female). As in most reptiles, growth continues throughout life with allometric changes in proportions. Head shape, especially, is subject to progressive change in males. With advanced age their jaws become elongated and heads are widened posteriorly (Fitch and Henderson, 1977).

Population Density: In the cemetery at Belize City, covering approximately 9.66 hectares, we recorded 49 ctenosaurs with total biomass calculated at 16.13 kg (1.67 kg per ha), adult females making up 45.2%, adult males 40.8% and first-year young 14.0%.

Although the cemetery superficially seemed to provide a fairly uniform habitat, the lizards were distributed with obvious clumping. As there was a surplus of food, the most obvious factor controlling distribution was relative age of gravestones in different parts of the cemetery. Where a high proportion of the stones were old, weathered, cracked, or partially collapsed, there were more hiding places for the ctenosaurs than there were where the stones were relatively new. Groups of graves that were enclosed by iron fences also seemed to provide security that made them especially attractive. There were four solitary individuals (subadult male, first-year young and two adult females) and 11 associations of from two to 10 individuals. The largest associations, with 10, eight and seven individuals, each had adults of both sexes and young. In associations of four, all were young. Associations of three had all young in one instance and had a pair of adults and a juvenile in another. Associations with only two lizards consisted of female and young in two instances, both young in two instances, subadult male and young in another.

Spacing between neighboring groups, or between groups and solitary individuals, averaged 74.5 m; within groups spacing of individuals averaged 25 m. Except in the case of consort pairs, it is doubtful whether individuals were attracted to others and the clumping observed may have been a result of the unevenly distributed resources, especially suitable shelter.

Taylor (1956) wrote that a colony of 10 or more ctenosaurs might be based at one large tree with hollow trunk or limbs. We found such a concentration would be unusual and would consist largely of immatures. An adult male and female often remain in close proximity for periods of days; otherwise individuals tend to be well spaced.

In Nicaragua, where ctenosaurs are extensively hunted, population densities comparable to that in the Belize City cemetery are unusual, but even higher concentrations were observed along roadsides, field edges and gullies in Chinandega Province north of Chinandega and along the Honduran border northeast of Palo Grande. In Costa Rica, similarly dense populations were observed at Finca Taboga in Guanacaste Province.

Because egg clutches are large, juveniles sometimes occur locally in high population densities. They tend to maintain spacing; aggressive displays and fights hasten their dispersal after hatching.

Population Structure: Ctenosaura similis normally requires nearly two years to attain sexual maturity, and individuals may survive and continue to grow for many years subsequently. A natural population therefore consists of many discrete annual age-classes, each larger in size and less numerous than the next younger group. Broods are large, but early mortality is heavy. Ratios of juveniles to older individuals are distorted by behavioral differences. Young that are several months old have become much like adults in behavior and habitat, and their cohorts have already sustained their heaviest losses.

Three separate population samples were obtained by different methods in the period February to April 1976, when first-year young were mostly in the age-range 8-10 months and had grown in linear dimensions to approximately three times their original size, and to approximately half the size of adults. These three samples (Fig. 2) show important similarities and differences, the latter probably reflecting biases inherent in the sampling techniques.

A sample of 160 ctenosaurs was obtained by hunting with a .22 rifle from a vehicle on roads and highways of Chinandega, León, Managua, and Chontales Provinces in Nicaragua. We attempted to obtain a random sample. However, there is a possibility of bias resulting from greater wariness of old individuals and/or from more persistent late afternoon activity in yearlings and gravid females. Numbers and percentages of different classes in the sample were as follows: first-year young 86 (53.6%); probable second-year adolescents 49 (30.6%); large adult males 7 (4.4%); large adult females 18 (11.3%). There were 32 males (135-220 mm) and 54 females (127-200 mm) in the group of first year-young, and 14 males (221-298 mm) and 35 females (201-250 mm) in the supposed second-year group. The adult males ranged from 299-400 mm, adult females from 253-295 mm. It is noteworthy that females constituted two-thirds of the total sample, and were from 63 to 72 per cent in different age-classes. Behavioral differences between adult males and females might cause some bias, but in first-year young sexual differences in behavior are small, if they exist at all, and would not result in significant bias. We therefore conclude that the sex ratio is strongly skewed in favor of females from the time of hatching.

A larger sample of 342 ctenosaurs was tallied from a vehicle during drives in the same parts of Nicaragua involved in the preceding sample. These animals were not handled; snout-vent lengths were merely estimated, and usually sex was not determined. Sometimes estimates were made simultaneously by two or three persons and a compromise figure was agreed upon. Often the same animal was first estimated and then shot and measured, providing opportunities for adjustment and refinement of the estimates. However, accuracy varied and for those only glimpsed briefly the range of error must have been relatively large. Large adults were better represented in this "sighted" sample, and first-year young were only 37.5% (vs. 53.6 in the "shot" sample).

A third population sample consisted of the 49 ctenosaurs observed at the Belize City cemetery 2-7 March 1976. Although only one was captured and measured, size estimates were made by observing them at close range and were checked repeatedly for most of them. Sex was readily distinguished in the full-grown lizards and tentatively distinguished in second-year adolescents (by head shape proportions, and elongated spine-like scales of the dorsal crest in the males) but could not be distinguished in first-year young. The latter averaged markedly smaller than first-year young in western Nicaragua at the same time of year, and unlike those young they did not overlap the second-year size-class. Of the 49 total, 27 (55.0%) were first-year young. Of the remaining 22, 8 (36.3%) were males and 14 (63.5%) were females. Five of the 8 males were large (320-400 mm) dominant individuals.

Figure 2 compares distribution of size-classes (with 25 mm interval) in each of the three samples. It shows that there is a continuum in size from the smallest first-year young to the largest adult males. Main concentrations are those of the first year young (150-200 mm in Nicaragua, but smaller in Belize) and of young adults (mostly females) 226-250 mm.

EXPLOITATION

The ctenosaur has delicate, tasty, white meat and in México and Central America it is much sought as an article of food. It is normally preferred over the iguana (*Iguana iguana*) where both occur together. However, in Belize only iguanas are eaten. In that region ctenosaurs are highly localized and because they are much in evidence in the Belize City cemetery, are regarded with a superstitious aversion. Called "wish-willys" by the English-speaking black Creoles, these reptiles are believed to feed upon corpses in the graves.

Elsewhere the species has probably been used for food since pre-Columbian times, but degree of exploitation varies locally. In parts of western Costa Rica where the ctenosaur is abundant, it is subject to little hunting, but in Nicaragua, El Salvador and Honduras it is intensively exploited and local populations have rapidly dwindled. We questioned many *campesinos* in western Nicaragua to obtain information concerning the time and amount of reduction. There was almost universal agreement that drastic reduction had occurred because of overhunting, but there was much difference of opinion, even in the same general area about the time of reduction. Many of the older *campesinos* who were questioned said that ctenosaurs formerly were numerous, but had become so scarce that now they are seldom hunted or eaten. Among 21 informants who had definite impressions as to when reductions had occurred, figures varied from 1 to 30 years, but 3 years was the most frequent estimate (6 instances) and the average was approximately 8 years.

Of 87 people questioned, 70 (80%) said they ate ctenosaurs regularly or occasionally. Most of these individuals or members of their families obtained the animals by hunting; a few bought their ctenosaurs from the hunter. Forty-nine persons made statements about the number of ctenosaurs eaten per week, which averaged 4.75. However, 17 other persons said they did not eat the meat, and 16 others who said they did (or had in the past) were vague about the amount because their use was occasional, rare or highly seasonal. Although our sample of interviews is small, and is doubtless biased in various ways it does indicate some general trends and suggests harvest on an enormous scale. Over extensive areas of western Nicaragua the majority of *campesino* families serve ctenosaur meat once to several times weekly, and this flesh is an important protein supplement to diets that otherwise tend to be high in starch and meager in quantity.

Hunting ctenosaurs is considered sport and the species qualifies as a game animal. *Campesinos* were questioned about their methods of capture. In order of frequency mentioned, the usual methods were: with a trained dog (52), with a noose placed at the burrow entrance or manipulated on the end of a long stick (24), with a slingshot (24), with a small bore rifle or pistol (9), and with a digging stick or shovel (6). Most informants mentioned 2 or more of these methods. For those that mentioned only one method, the order and number were: dog (12), slingshot (3), digging (2), gun (2). Sunday hunting is customary, especially for persons who work during the week, as field hands on *fincas;* it is often the main outdoor recreation.

In some areas, *campesinos* from early childhood develop a familiarity with ctenosaurs and the techniques of taking them. Certain families and even communities specialize in hunting the lizards, make it their main occupation and supply the market places. The villages of Palo Grande, Somotillo and Villa Nueva near the Honduran border have many hunters who are the main suppliers of the market in Chinandega and contribute to the stocks in León, Managua, Masaya and Granada. Several other villages in northwestern Nicaragua are also important suppliers: Somoto (for Chinandega), and Rota and El Sauce (for León). Most of the ctenosaurs sold in the Mercado Oriental of Managua were said to have come from the village of San Francisco de Carnicera on the northeastern shore of Lake Managua. However, the ctenosaurs shipped from San Francisco are assembled by a dealer there from the neighborhood of Cuatros Palos and other outlying villages farther north and east, and represent the combined efforts of approximately 20 hunters. Professional hunters are especially skilled, not only in finding and capturing the animals, but in taking them alive and intact. One hunter demonstrated his technique, with a long bamboo pole having a cord noose at the end, and a bait of calf liver suspended in front of it. He told us that with his partner he left home for as much as 3 days at a time on extended hunts to areas several kilometers away, where the lizards were still relatively numerous, and both men returned heavily loaded with sacks of live ctenosaurs.

A few dozen skilled hunters are the main suppliers of the market in the larger Nicaraguan cities. They hunt on foot and their activities are concentrated in relatively small areas where ctenosaurs are abundant. Each hunter captures dozens of the animals weekly, but some men limit their hunting to the lizards' reproductive period, December through April, and seek other means of livelihood for the remainder of the year.

In February and March 1976, there were usually 1 to 5 vendors selling ctenosaurs at each major *mercado* in Nacaragua. Occasionally a vendor had between 100 and 200 ctenosaurs at one time, but usually the stock was much less— sometimes only one. The vendor normally replenished his stock with a new shipment once or twice a week. Often the shipment consisted of a mixed lot of ctenosaurs and iguanas. Some of the animals were kept in gunny sacks, while others were displayed in large wicker baskets, or were strewn over the sidewalk, immobolized by having their feet bound behind them. The live animals attracted considerable attention from passing crowds. When a new lot was displayed, prospective buyers gathered to examine and handle the animals, with brisk trading favoring egg-bearing females and large, fleshy males. At the two *mercados* in León, live ctenosaurs were usually absent or were displayed in small numbers, but the dressed carcasses were sold at several indoor stalls. Piles of several dozen carcasses were on display on most occasions. We were told that the butchering was done at the home of the vendor, in pre-dawn hours before the *mercado* opened. At other *mercados* dressed ctenosaurs were seen in small numbers, but most of the animals were sold alive.

From the numbers of ctenosaurs appearing at Nicaraguan *mercados,* and from the statements of vendors, the aggregate weekly consumption must total hundreds of animals. Chinandega, León, Masaya, Managua, and Granada rank in about that order in numbers consumed. Many other small towns and villages participate in the ctenosaur trade, but on a relatively small scale. Some of the villages in northwestern Nicaragua that supply major *mercados* export part of their stock to El Salvador. Trucks with shipments of hundreds cross the border into Honduras from Somotillo and El Espino, Nicaragua, and hundreds more are sent by ferry from Potosí directly to El Salvador at Puerta Amapala. Nevertheless, the commercial harvest seems to be much less than the aggregate harvest by individuals hunting for family subsistence.

Live ctenosaurs were sold for food in 1976 at prices ranging from 1.5 Cordobas to 15 Cordobas (1 C = $0.14 US). The lowest prices prevailed in the villages of northwestern Nicaragua. There the hunters usually received 2 or 2.50 C apiece for ctenosaurs and sold them in dozen lots. In other parts of the country where the animals were less common, the hunters usually received 3 or 4 C apiece for them. The buyer usually paid 5 C at the Chinandega *mercado,* 8 (7-10) at Managua and 8-12 at Masaya and Granada. At the latter two cities, there was often an adjustment of price according to the animal's size, whereas at Chinandega the price tended to be uniform even though one animal might be as much as 5 times the bulk of another.

DISCUSSION

Ctenosaura similis is unique among American lizards in several aspects of its ecology: It has become adapted as an adult to feed upon the dominant vegetation, with the result that food supply is not generally limiting. It produces remarkably large egg clutches (mean 43.4, maximum at least 88). It is single-brooded with eggs laid late in the dry season and young appearing early in the rainy season. Its hatchlings are remarkbaly small compared with adults (about 16 per cent of female length and one per cent of female weight). Its females are much smaller than males (80% of male length and 55.6% of male weight) and are more numerous both in samples of adults and in first-year young in a ratio of about 2 to 1. Sexual maturity is attained late in the second year, and the two-year-old primiparae made up 23.2% of the breeding females and produced 10.6% of the eggs in a sample.

Although the ctenosaur is "*K*-selected" (see Pianka, 1970) in having a long life expectancy, postponing maturity till the second year, and producing a single annual brood, it is "*r*-selected" in its remarkably large clutch, in relatively small size of its eggs and hatchlings, and in its adaptation to disturbed and seral habitats. All these "*r*-selected" traits reduce its vulnerability to exploitation by humans and confer potential as a successful game animal. Over extensive areas of xeric habitat where the original fauna has been depleted by man-made changes, involving virtual elimination of the birds and mammals that were favorite game animals, the ctenosaur continues to thrive. Heavy grazing, or clearing of the land for cultivation, favor its survival and increase if there are certain essential habitat features that assure adequate shelter and a year-round food supply.

Despite its high reproductive potential and capacity to withstand hunting pressure, the ctenosaur has had its populations reduced at an accelerating rate in recent years. Mushrooming human populations have resulted in ever-increasing hunting pressure, with hunting intensified in the season of reproduction and concentrated on the gravid females, the least expendable part of the population. The reduction that has already occurred must have involved annual loss of hundreds of tons of high grade protein food in Nicaragua alone, with the prospect of increasing losses until the yield becomes negligible. Management practices that will reverse the trend are acutely needed.

It would be easy to suggest measures that would preserve remaining populations and permit their increase, but it is much more difficult to make practical recommendations. Exploitation of the ctenosaur is deeply rooted in tradition, whereas the concept of conservation is foreign to the exploiters. In the face of want, *campesinos* will not readily relinquish their presumed right to hunt ctenosaurs for food or to harvest the gravid females that should be left to replenish the population. Elimination of this potentially valuable species is deplorable and unnecessary. There are slight grounds for optimism in the fact that rural people almost universally recognize that ctenosaurs are rapidly becoming scarcer and that this decline results from overhunting.

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